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BREEDING BLISTER RUST RESISTANT WESTERN WHITE PINE.
Part 6 ~~VI.~~ FIRST RESULTS FROM FIELD TESTING OF RESISTANT PLANTING STOCK

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ABSTRACT

Twenty- to 36-acre pilot-scale tests for determination of "field" resistance in blister rust resistant western white pine have been established in three localities in northern Idaho and northeastern Washington. The F_1, B_1, and F_2 planting stocks represent, respectively, one, one and one-half, and two cycles of selection for general combining ability for resistance. Preliminary results from the first-planted, 36-acre test, following natural exposure to the rust for 2 years, in a locality of extremely high blister rust hazard, showed nonresistant control stock 76 percent infected, with 2.66 cankers per infected tree. The F_1's were 31 percent infected, with 1.56 cankers per tree; B_1's, 24 percent infected, with 1.45 cankers; and F_2's 12 percent infected, with 1.19 cankers. Companion experimental tests of similar F_1 and F_2 progenies artificially inoculated at age 2 years in the rust nursery showed that at 30 months after inoculation F_1's were 67 percent infected, F_2's 34 percent infected. Thus, field tests were confirmatory of nursery tests. There is good expectation for attaining similar, and probably longer lasting performance, in F_2 planting stocks soon to come from production F_2 seed orchards now in the process of establishment.

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KEYWORDS: breeding methods (plant), selection (artificial), disease resistance, western white pine (*Pinus monticola*), white pine blister rust (*Cronartium ribicola*)

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BACKGROUND

Since 1950, a research and development program toward production of blister rust resistant western white pine planting stock has been conducted by the Intermountain Station and the Northern Region. Progress of the work has been reported from time to time.

Bingham (1954) covered first results in 60 first-generation (F_1) progenies from crosses between rust-free "candidate trees" found in rust-decimated natural stands. The 2-year-old progenies were artificially inoculated. Proportion of seedlings with foliar infections ranged from 47 to 97 percent, and the frequency of needle lesions from 37 to 402 per 450 needles. By 1957, following the single inoculation, and after the rust had fairly well run its course in these F_1 progenies, Bingham, and others (1960) showed that resistance was definitely seed transmissible--from rust-free candidates to F_1 offspring. They also showed that about one in four candidates tested had general combining ability (GCA) for resistance, that is, they consistently transmitted above-average levels of resistance to a number of their F_1 progenies. Furthermore, when two such GCA trees were mated, about 30 percent of the seedlings in the resulting GCA-F_1 progenies somehow withstood the intense, artificial exposure to the rust. Three or more possible mechanisms and seats of resistance were recognized: (1) a mechanism that reduced the number of stomatal penetrations or prevented establishment of rust mycelium in the needles; (2) a mechanism(s) that prevented rust mycelium from invading or establishing itself in branch or stem bark from infected needles; and (3) a mechanism(s) in the bark that eliminated the rust after successful invasion of the stem.

Our first results on field resistance were reported by Steinhoff (1971). He showed that after 11 to 15 years exposure to apparently moderate, natural blister rust inoculation on two experimental forest field plots in northern Idaho, 40 small GCA-F_1 progenies became 20 percent infected, planted controls 58 percent infected, and naturally reproduced white pines of about the same age 71 percent infected.

Early heritability and genetic gain analyses (Bingham and others 1960) were favorable. Heritability (h^2) of resistance was estimated at about 70 percent, and substantial gains of about 20 percent were forecast should selection for GCA proceed through a second cycle of breeding. Thus, F_2 progenies bred from tested, resistant GCA-F_1 trees should approach 50 percent resistance. Cooperators accepted this predicted level of resistance as sufficient for a first-stage program in which F_2 planting stock would be produced in F_1 seedling orchards.

A period of intensified developmental work followed in 1960-1972. Cooperators screened 400 candidates for GCA, and selected the best 24 GCA-trees in each of the low-, mid-, and high-elevation planting zones for the species. Then they remated pairs of the 24 GCA trees from each zone, thus producing 12 large GCA-F_1 families per zone. Finally, they artificially inoculated the 36 families, selecting sufficient numbers of resistant, GCA-F_1 seedlings to establish 12-family seedling seed orchards for each elevational zone. Now, 13 acres of low-elevation orchard, 20 acres of mid-elevation orchard, and 7 acres of high-elevation orchard--acreage varying according to anticipated National Forest planting-site elevations--are being established near Coeur d'Alene, Idaho. Significant production of F_2 seed is anticipated about 1985.

Thus results from nursery and field testing of F_2 seedlings are of particular importance to the Station-Region first-stage program. The F_2 tests are proceeding in two places: (1) in the blister rust nursery, under artificial inoculation, at Moscow, Idaho; and (2) on 20- to 36-acre pilot-scale field plantings, under natural inoculation, on three nearby National Forests in northern Idaho and northeastern Washington. Results from (1), above, have been reported by Hoff and others (1973). The present Research Note describes the earliest preliminary results from a field plot planted in 1970 on the St. Joe National Forest.

MATERIALS AND METHODS

The results reported here are from a study entitled "Field Level of Resistance in Stocks from Early-Generation Breeding" and including F_1, F_1 backcross, and F_2 progenies, as well as local-origin, nonresistant control seedlings. Combinations of all of these early-generation progenies were planted in two identically designed, 36-acre field plots, one on the St. Joe National Forest near Clarkia, Idaho (1970, West Fork, Merry Creek) and one on the Colville National Forest near Newport, Washington (1971, Gletty Creek). One 20-acre planting, using only F_2 and local control progenies in mixed-species plantings with local Douglas-fir and grand fir, has also been established on the Clearwater National Forest near Pierce, Idaho (1972, Jaype). Materials, methods, and results given below apply only to the 36-acre field plot on the St. Joe National Forest.

Seed, Pregermination Treatment, and Nursery Sowing

Since 1950, surplus seeds from many different early-generation crosses have been stored in airtight containers at 35° to 40° F at our Moscow, Idaho, laboratory. This seed is of three types: F_1, from crosses between two natural-stand GCA trees; B_1, from crosses between 10- to 15-year-old resistant GCA-F_1 arboretum trees as seed parents and nonrelated natural-stand GCA trees as pollen parents (that is, P_1 X P_0 backcrosses), or F_2, from crosses between two nonrelated resistant GCA-F_1 trees in the arboretum. The three types of "resistant" seed thus represent results of one, one and one-half, and two cycles of selection for GCA.

Three bulked seed lots representing the three kinds of resistant seed were compounded for the St. Joe National Forest field plot by mixing from 40 to 80 individual seed lots. These bulks, along with a nonresistant control seed lot, are characterized in table 1.

Table 1.--*Composition of bulked seed lots field tested on St. Joe National Forest plot*

Type of bulk	Individual lots included	Seeds per lot, range	Total seed	Parentage			Crosses of different pedigree represented	Selection areas represented	Elevation range, GCA trees
				GCA trees	CGA-F_1 families	Trees per family, range			
									Feet
F_1	61	16- 1,303	20,038	30			61	12	2,675- 4,100
B_1	83	3- 765	15,019	13	27	1-7	40	4	3,020- 3,200
F_2	43	2- 2,318	9,997	9	18	1-6	34	4	3,020- 3,200
Control	[1]1								

[1] U.S. Forest Service Northern Region, seed lot 18-0-119-4, St. Joe National Forest origin.

After brief infrared irradiation (cf. Works and Boyd 1972), the three resistant seed bulks were "naked-stratified" in covered flasks at 35° to 40° F, for 50 days during April and May 1967. At the end of May, seed was broken out and dusted with 50 percent wettable Captan, then surface dried. Each bulk was divided into 30 roughly equal parts by weight and then returned to the refrigerator in small polyethylene bags. The next day, seed was transported to the Forest Service nursery at Coeur d'Alene, Idaho, and carefully broadcast sown. Spacing was close to 2 by 2 inches. Sowing was in three randomized complete blocks making up one 315-foot-long nursery bed. (The bed had been fumigated with methyl bromide:chloropicrin, 2:1.) To secure seed spacing, bedspace allotted to a given bulk in each block was divided into 10 equal parts, and the seed from one of the 30 polyethylene bags was sown in each of the 30 parts of the nursery beds. For the control group, 1-year-old plants in a standard nursery bed at the Forest Service's former Savenac Nursery at Haugan, Montana, were used. The plants were raised from the only available St. Joe National Forest seed of the same geographic and elevational zone as the proposed outplanting area, sown in fall 1965. We elected to use this 1-year-older stock rather than risk maladaptation possibly associated with use of control stock from a different geographic or elevational zone.

Nursery Tending, Lifting, and Planting

Stock remained in the two nurseries under routine fertilizing and overhead irrigation regimes through spring 1970. By then the three resistant stocks were 3-0 age, and about to commence their fourth season of growth; control stock was 4-0, and entering its fifth season. Early in April, seedlings were undercut, lifted, root-pruned to 12 inches, bundled, counted, tagged, packaged in polyethylene-treated cardboard boxes with moist sphagnum moss around the roots, and stored in the seedling storage refrigerators at Coeur d'Alene. Packaged stock was delivered by refrigerated truck to the Clarkia Ranger Station, Clarkia, Idaho, on May 4, 1970, and stored there in a walk-in refrigerator at 40° F until outplanted May 5 to 21.

The 36-acre planting area in the West Fork of Merry Creek (about 4 miles NNE. of Clarkia, Idaho, mean elevation about 3,600 feet) had been clearcut and burned in the fall of 1968. In the experimental design used in planting (fig. 1), there are three 3- by 4-acre blocks (A, B, and C), and within each block there are three 1- by 4-acre replicates (1, 2, and 3). Each replicate contains one acre-sized planting (210 by 210 feet) of each of the resistant and control stocks. Spacing of planting stock varied from 7 by 7 feet to 9 by 9 feet (fig. 1), depending on the expected rust mortality of the different resistant stocks, or the amount of control stock available. In each acre planting, the North-South rows of trees were planted in almost perfectly straight rows, using portable, stretchable, bungee-cord lines to mark the row while it was planted. Under the bungee-cord line, holes 12 inches deep and 4 inches wide were bored with a gasoline-powered planting auger. Color-coded tape markers were used on the cord at 7-, 8-, or 9-foot intervals; holes were allowed to vary up to 2 feet either way along the line from the markers, but not to left or right of the line. This procedure was followed to insure that planted white pines would be distinguishable from naturally reproduced white pines for many years.

After root pruning, the three types of resistant planting stock had a normal (about 2:1) root:shoot ratio, but the 1-year-older control stock from more crowded nursery beds had somewhat "leggy" tops, fewer fibrous roots, and more tap roots. Less than 1 percent of the 23,700 planting spots on the 36-acre plot (180) were not planted; about three-fourths of the unplanted spots were in swampy areas, and one-fourth under logs or stumps lying along the straight planting lines.

In September 1972, permanent sample trees were chosen, tagged, and examined. In each acre area, 25 trees were chosen in four clusters of six or seven trees. The

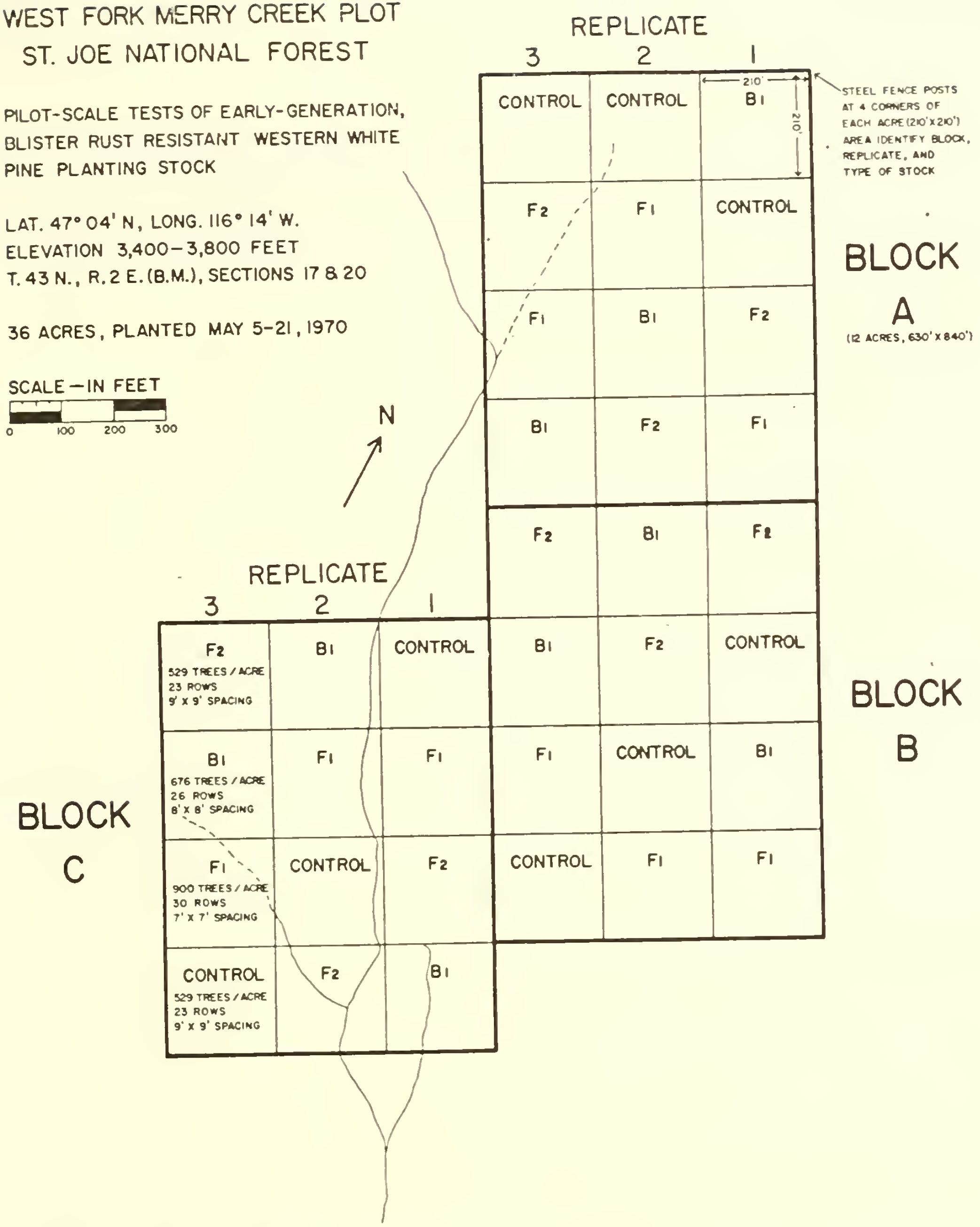

Figure 1.--The 36-acre field test planting, consisting of three randomized blocks.

cluster center was the planting spot three rows and tiers into the acre plot, at each corner. Thus, in each 4-acre replicate there were 100 sample trees, making 225 sample trees per stock type, 300 per block, and 900 total. Data recorded for each sample seedling were (1) planting row and tier (row 1 tier 1 being the position nearest the acre's northwest corner post); (2) height in centimeters; and (3) the number of stem and the number of branch cankers.

One year after burning (fall 1969), a very heavy crop of seedlings of the sticky currant (*Ribes viscosissimum* Pursh) was present on the area. During planting (spring 1970), it was noted that these plants had persisted and were particularly abundant

along the ridges. The largest currant plants were then 35 cm tall and had up to 125 cm of live stem. By the time of sample-tree examination (fall 1972), the largest currant plants were 75 cm tall, with 250 to 300 cm of live stem. *Cronartium ribicola* J. C. Fisch. ex Rabenh., in the uredial or telial stage, was observed to be abundant on undersides of the currant leaves in both 1970 and 1972.

RESULTS

Planting Survival

Checked in late September 1970 after the first summer, which was somewhat rainy and thus favorable for seedling establishment, survival in the four types of stock was, for controls, 62 percent; F_1's, 93 percent; B_1's, 82 percent; and F_2's, 92 percent. This left about 9,750 planted trees on the 36 acres.

Blister Rust Infection

The 1972 inspection yielded means for each of the thirty-six 25-tree or acre samples as shown in table 2. A glance at these basic data, and at the grand means (table 3), shows the relatively wide range of variation in rust intensity, and possibly seedling height, associated with blocks, replicates, and stock types. The main differences emerging after only 2 years of natural rust exposure seem to be associated with type of planting stock. For example, control stock is much more heavily infected than are the three resistant stocks (table 3). Sixty-four percent more (six times as many) control seedlings than F_2's are infected, and these infected plants bear 2.2 times as many cankers as infected F_2 plants. Fifty-two percent more (three times as many) controls than B_1's are infected with 1.8 times more cankers per infected tree; and 45 percent (two and one-half times as many) more controls than F_1's are infected, with 1.7 times more cankers per tree.

The analysis of variance (table 4) shows that stock types differ significantly in percent infection and numbers of cankers per infected or sample tree. Also, there are significant stock type X block interactions affecting cankers per tree, or height of healthy trees. This might be expected in view of the epidemiological and silvical contrasts that could occur between such large (12-acre) blocks. The Scheffé S-contrast test (table 5) shows that there is significant variation among the four stock types. Controls are significantly more heavily infected than the three resistant stocks, and F_1 stock is significantly more heavily infected than F_2 stock.

Seedling height was considered because there may be positive correlation between height (an indirect measure of foliation, or target area presented to airborne rust basidiospores) and the number of blister rust cankers per tree. This relationship has been suggested for both western and eastern white pines (Childs and Kimmey 1938; Filler 1933). In fact, when a correlation analysis is applied to the data of Childs and Kimmey (1938, table 4) for mean tree height vs. average number of cankers per tree, a high correlation of these two variables ($r = 0.976$, significant at the 1 percent level of probability) is evident. It seems likely that a similar relationship holds for unpublished individual-tree data of the above report. Thus it is a tenable assumption that environmentally or genetically controlled increases in tree height may be accompanied by increases in the number of cankers per tree. It is pertinent to investigate any extraneous differences in tree height that might be associated with sample tree age (controls are 1 year older), with rate of height growth between the genetically different types of stock, or with blocks and replicates within blocks.

Table 2.--*Mean blister rust infection and tree height in the field test plot, St. Joe National Forest, by type of planting stock, blocks, and replicates*[1]

Type of stock, block, and replicate	Infection per 25-tree sample	Total cankers on infected trees	Average cankers per infected tree	Average cankers per sample tree	Height of average infected tree	Height of average healthy tree
	Percent				- - - - *Cm*	- - - -
Control						
A1	92	58	2.52	2.32	34.3	30.0
A2	96	73	3.04	2.92	42.0	40.0
A3	88	79	3.59	3.16	46.9	40.0
B1	64	38	2.38	1.52	35.9	33.0
B2	76	34	1.79	1.36	33.6	37.7
B3	48	21	1.75	0.84	37.8	37.2
C1	88	53	2.41	2.12	42.6	38.5
C2	72	65	3.61	2.60	41.2	41.5
C3	60	43	2.87	1.72	34.5	33.6
F_1						
A1	16	6	1.50	0.24	50.2	42.7
A2	40	19	1.90	0.76	39.3	43.1
A3	56	37	2.64	1.48	46.9	45.0
B1	28	10	1.43	0.40	38.6	32.9
B2	28	7	1.00	0.28	36.6	37.7
B3	20	7	1.40	0.28	45.2	40.7
C1	36	9	1.00	0.36	38.6	34.4
C2	48	19	1.68	0.76	38.5	28.8
C3	8	3	1.50	0.12	43.0	35.8
B_1						
A1	8	3	1.50	0.12	37.5	35.9
A2	36	14	1.56	0.56	28.3	35.6
A3	32	14	1.75	0.56	37.6	34.9
B1	20	10	2.00	0.40	48.2	39.1
B2	28	10	1.47	0.40	37.0	44.1
B3	20	4	1.00	0.16	32.3	35.1
C1	12	3	1.00	0.12	44.5	41.4
C2	28	11	1.57	0.44	35.0	35.5
C3	36	11	1.22	0.44	38.6	34.4
F_2						
A1	12	3	1.00	0.12	28.7	29.7
A2	12	3	1.00	0.12	37.0	27.6
A3	24	10	1.67	0.40	33.6	33.5
B1	8	3	1.50	0.12	61.0	37.2
B2	28	11	1.57	0.44	37.9	36.4
B3	4	1	1.00	0.04	48.0	37.5
C1	4	1	1.00	0.04	32.0	31.4
C2	4	1	1.00	0.04	49.0	33.3
C3	12	3	1.00	0.12	44.0	33.0

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[1] Data cover 25 sample trees from each acre of plantation.

Table 3.--*Grand means for blister rust infection and tree height according to blocks, replicates, and stock types, field test, St. Joe National Forest*

Variable	Infection per 25-tree sample	Angle = arcsin $\sqrt{\%\ \text{inf.}}$[1]	Cankers per infected tree	Cankers per sample tree	Height of average infected tree	Height of average healthy tree
	Percent				*Cm*	*Cm*
Blocks						
A	42.7	40.89	1.97	1.06	39.9	36.5
B	30.7	32.76	1.52	0.52	38.2	37.4
C	34.0	34.01	1.66	0.74	39.1	35.1
Replicates						
1	32.3	33.36	1.60	0.66	39.4	35.5
2	41.3	39.73	1.76	0.89	37.7	36.8
3	33.7	34.57	1.78	0.78	40.8	36.7
Stock types						
Control	76.0	62.00	2.66	2.06	38.8	36.8
F_1	31.1	33.21	1.56	0.52	41.9	37.9
B_1	24.0	29.10	1.45	0.36	37.7	37.3
F_2	12.0	19.24	1.19	0.16	41.2	33.3
Overall means	35.7	35.88	1.72	0.77	39.9	36.3

[1] Transformation of percentage (binomial) data recommended by Bartlett (1936) to stabilize variances, and used in analyses of tables 4 and 5.

Table 4.--*Significance of overall differences for stock types, block, and replicates by analysis of variance, field test, St. Joe National Forest*

Source of variation	MS[1] tester	Degrees of freedom	Angle = arcsin $\sqrt{\%\ \text{inf.}}$		Cankers per infected tree		Cankers per sample tree		Height of average infected tree		Height of average healthy tree	
			MS	F[2]	MS	F	MS	F	MS	F	MS	F
									- - - - - Cm	- - - - -	- - - Cm	- - -
1. Blocks	2.	2	228.18	1.996	0.561	1.276	0.896	3.588	19.12	0.483	15.42	1.468
2. Replicates within blocks	6.	6	114.33	0.337	0.440	0.829	0.250	0.323	39.60	0.885	10.50	0.564
3. Stock types	4.	3	3036.24	40.132**	3,786	9.713*	6.828	17,209**	35.75	0.438	38.92	0.969
4. Stock type X blocks	5.	6	75.66	1.168	0.390	6.168**	0.397	8.000*	81.52	2.115	40.16	3.608*
5. Stock type X replicates within blocks	6.	18	64.76	0.190	0.063	0.119	0.050	0.064	38.55	0.861	11.13	0.597
6. Total		35	339.16		0.531		0.773		44.75		18.63	

[1] Mean square.
[2] Fisher's variance ratio.

*Significant at the 5 percent level of probability.
**Significant at the 1 percent level of probability.

Table 5.--*Significance of differences between pairs of stock type means by the Scheffé (1959) S-contrast test, field test, St. Joe National Forest*

For difference between			F, Fisher's variance ratio				
			Angle = arcsin $\sqrt{\%\ \text{inf.}}$	Cankers per infected tree	Cankers per sample tree	Height of average infected tree	Height of average healthy tree
						Cm	*Cm*
Control	and	F_1	14.405**	8.020**	17.336**	0.316	0.108
		B_1	18,811**	9.704**	21.126**	0.040	0.022
		F_2	31.776**	14.323**	26.389**	0.190	1.099
F_1	and	B_1	0.294	0.802	0.187	0.580	0.032
		F_2	3.392*	0.907	0.947	0.016	1.898
B_1	and	F_2	1.690	0.448	0.292	0.403	1.435

*Significant at the 5 percent level of probability.
**Significant at the 1 percent level of probability.

The analysis of variance (table 4), however, shows that there are no significant relationships of tree heights with blocks, replicates, or stock types. Height of the average healthy (but not infected) tree is significantly affected by interaction of stock type and block. Similarly, the Scheffé test shows no significant differences in height across the four stock types. Finally, to examine more directly the possible relationship between seedling height and cankering, the individual infected-tree heights and numbers of cankers were used in correlation analyses for each of the four stock types. The results were:

Stock type	*Infected trees*	*Correlation coefficient (r)*
Control	152	0.245**
F_1	69	.234
B_1	50	-.124
F_2	24	-.132

**Significant at 1 percent level of probability.

The low, or nonsignificant correlation coefficients provided by these latter analyses tend to support the interpretation arrived at from results of the analysis of variance and Scheffé S-contrast tests--that is, there is a general uniformity of tree heights, thus lack of extraneous height effects, across blocks, replicates, and stock types.

DISCUSSION AND CONCLUSIONS

Hoff and others (1973) demonstrated that in nursery trials where progenies were artificially inoculated at 2 years of age, 90 to 100 percent of the seedlings developed foliar infections. However, 30 months later 33 percent of the GCA-F_1, and 66 percent of the GCA-F_2 seedlings were free of rust. What is the equivalence of such "rust nursery resistance" and "field resistance" that would be apparent after long-continued exposure of GCA-F_1's and F_2's to natural inoculation in the forest? The Note by Steinhoff (1971) covering 40 small GCA-F_1 progenies exposed in two field plots to moderate levels of natural inoculation, reported that GCA-F_1's performed well after 11 to 15 years of exposure.

Newer information from large F_1, B_1, and F_2 progenies given here is even more encouraging. At this early date, resistant progenies show excellent performance in a single, 36-acre high-rust-hazard area. After 2 years of natural exposure to blister rust, 88 percent of the F_2's, 76 percent of the B_1's, and 69 percent of the F_1's, but only 24 percent of the controls, remain free of rust. Progressive accumulation of resistance from one cycle (F_1's), one and one-half cycles (B_1's), and two cycles (F_2's) of selection for general combining ability is apparent. The accumulated resistance may of course prove transient if rust race population structure changes, and it may diminish substantially between juvenile and rotation age. If not, however, the F_2 stocks soon to come from the Coeur d'Alene seed orchards will indeed be useful.

Two indications of the probable stability of rust resistance should be noted. First, on the forest areas where parental candidates are located, blister rust has been present about 45 years. Candidates found to be free of rust up to 1950 have remained so. Thus far, no visible changes in the rust population have occurred, despite intense natural selection proceeding in northern Idaho forests. In addition, seed orchard F_2's will probably have a more stable genetic base in resistance than the field-tested F_2's discussed here, which were developed under "blind" selection for GCA. That is, resistant GCA-F_1 foundation stocks were selected merely because they survived intense, artificial exposure to the rust. They were crossed in the arboretum without knowledge of the kinds or numbers of resistance genes and reactions they might represent. One result of this blind selection, as Hoff and others (1973) have shown, was that about seven-tenths of the resistance apparently came from a single, immunity-imparting recessive gene. They pointed out, however, that proportions of resistance owing to this or to other major or minor genes in the F_2, could be substantially altered, or equalized, through use of newer information when selecting resistant F_1 foundation stocks for seed orchards. This newer information on foliar and bark resistance genes and reactions was utilized in selection of the Coeur d'Alene orchard foundation stocks. Presumably, the more broadly based F_2 stocks to come from these orchards will embody more stable resistance than the blindly selected F_2's now being field-tested.

On this basis, can we conclude that the blister rust problem is solved for western white pine? For the time being the answer has to be "no." The first-stage, resistant F_2 stock (potentially about 65 percent resistant) appears to be a good *first* product--one that has good possibility for restoring the silviculturally tractable and valuable western white pine as a manageable component of the ecosystem for a rotation or more. Nevertheless, we realize that we now must work toward stabilizing resistance. Cooperators in this breeding venture agree that first-stage F_2 seed should not be planted for more than about 20 years, and then only in mixed plantings with other competitive, native species. Accordingly, first-stage seed orchards planned to meet all Northern Region National Forest requirements for western white pine are relatively small (40 acres). With mixed species planting, these orchards will provide seed for planting 15,000 to 20,000 acres per year.

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